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STERILITY AND FERTILITY IN SPECIES OF HEMEROCALLIS

For a number of years problems of fertility and sterility in numerous species of plants that freely and naturally propagate by vegetative means have been under investigation by the writer. In these studies several species of *Hemerocallis* have received considerable attention, and a brief preliminary report of the results obtained with them has been given (Journal N. Y. Bot. Garden 20: 104–105, May, 1919). Certain aspects of the research await the blooming of seedlings that are now being grown and the testing of wild plants of several species which it is hoped can be obtained from their native home in the orient. But the results already obtained, and in part published, supplement and to some degree extend the observations recorded in a recent number of the Torreya (21: 12–13, Jan. and Feb. 1921) and for this reason may be briefly summarized for the readers of this journal.

It is to be noted that the double-flowered form of *Hemerocallis fulva* reported in Torreya (18: 242) and referred to later (Torreya 21: 13) is undoubtedly an old and well known sort. A double-flowered variety of this species is reported by Thunberg in his Flora Japonica published in 1784 and there identified as the double-flowered plant which Kaempfer (Amoen. Exot. 1712) thought was an *Iris*. At the present time two double-flowered varieties are recognized (Bailey, Cyclopaedia of Horticulture) as belonging to *H. fulva*. One of these, var. *Kwanso*, is illustrated in color in Gartenflora in 1866 (plate 500) and there said to have been introduced into Europe by von Siebold. This is evidently the double-flowered form most widely found in cultivation in Europe and America. The other variety (*flora plena*) is illustrated in color in Flora des Serres

(1869–1870) and there called *H. disticha* var. *flora plena* (*disticha* is now considered as a synonym of *fulva*). The colored plate shows this to be quite different from var. *Kwanso* in appearance. The writer has never seen this variety. A double-flowered variety has also long been known in the species *H. Dumortierii*.

A thorough search of the literature indicates that no one has ever reported fruit on the single-flowered type of *H. fulva*. This orange-colored day lily is widely distributed over Europe and America. Its complete failure to produce fruit and seeds has often been noted. Only one variety of it (var. *maculata*) appears to have been involved (probably as a pollen parent) in the production of hybrids.

In the writer's experiments with this species many intra-specific pollinations have been made between plants obtained from such widely different sources as Wisconsin, Michigan, New York, Vermont and England with complete failure in every case. The ovaries of flowers thus pollinated do not start to enlarge, and about 72 hours after the flowers open the entire flower falls leaving only spurs as shown at *a* in Fig. 4.

But the pollen of this species used in controlled crossing on *H. flava* has given pods (Fig. 2) with seeds and the hybrids resulting are now being grown. The reciprocal cross between these two species failed to yield mature pods. Pollen of *H. fulva* on *H. minor* has given seed but no germination was secured.

Pollen of *H. Thunbergii* and of *H. aurantiaca* has been used on many flowers of *H. fulva*. Usually the pods begin to form and seeds start to develop with some of them, but as a rule the pods fall when about one third mature (*b* in Fig. 4). In a few instances, however, mature pods with ripe seeds (Fig. 5) have been secured, but no germination has yet been obtained in such seeds. The reciprocals of these crosses likewise produce seed rarely. From the results of crossing *H. fulva* with *H. flava*, *H. aurantiaca* and *H. Thunbergii* it appears that its pollen and ovules are potent and are able to function in certain relations, but that the compatibility in these combinations is of a weak grade.

The literature gives conflicting reports regarding seed production in *H. flava*. Some investigators have reported plants of it to be self-fertile, others have reported the plants they have studied to be self-sterile. Both self-compatible and self-incompatible plants have been found among plants of this species grown in the New York Botanical Garden. Such conditions are often seen in a species in which self-incompatibility is present, especially if the species is propagated by seed (*Cichorium Intybus, Nicotiana Forgetiana, Eschscholtzia californica, Brassica pekinensis, Brassica chinensis,* and others). The most highly self-compatible plants produce pods in abundance, but in them are many shrivelled ovules in which fertilization may not have occurred and seeds in various stages of embryo abortion together with seeds that are fully matured and viable (Fig. 3). This condition is also specially characteristic of plants that are not fully self-compatible.

A third species, *H. Thunbergii*, has in the author's experience proved to be only feebly self-compatible. Very many carefully made self-pollinations fail (see 6, 7 and 8), but many pods do mature and these contain some seeds which will germinate. All the plants of this species which are growing in the New York Botanical Garden have behaved quite the same, but these may have all descended from a single parent through vegetative propagation. A wide range of self-compatibility may be exhibited by the seedlings which are to be tested as soon as they bloom.

The type of sterility in these species is, undoubtedly, that of physiological incompatibility operating between the organs concerned in sexual reproduction. The readiness with which these species propagate from pieces of the roots and by rhizomes has practically eliminated the use of seeds in commercial propagation. Such a method tends to perpetuate the grade of self-compatibility of the original plant which was used. It is possible that the plants of the single-flowered type of *fulva* now growing in America and Europe may have all come by vegetative propagation from a single plant which happened to be fully self-in-

compatible. According to Clusius (*Plantarum Historia,* p. 137) this species was commonly in cultivation in middle Europe as early as 1601. Since then its cultivation has been extended over large areas of Europe and America, and in many sections it has escaped from cultivation and is spreading widely, purely by vegetative means of propagation.

It can be predicted with confidence that a search in the region where *H. fulva* is native and wild will reveal plants that are producing seed or at least strains that will prove compatible with the self-incompatible strain now found in the United States. Focke showed that such a condition as this existed in *Lilium bulbiferum.* After failing for years to get seed by selfing and crossing plants of this species obtained from various parts of Germany, he obtained wild plants from the native habitat in Tyrol and these he found compatible with strains that previously failed to produce seed.

It has very generally been held that the seed sterility of such plants as *Hemerocallis fulva, Lilium bulbiferum, Lilium tigrinum,* etc., is "correlative." That is, the vegetative organs of propagation are conceived to divert and utilize the available food so that the embryos in seeds are virtually starved to death during stages in development, or perhaps organs are so poorly nourished that they do not function previous to fertilization. But evidence is increasing to the effect that seed production in these plants is relative and depends on whether fertilizations are compatible, quite as is the case in numerous species of plants that are naturally propagated only by seeds. The experimental proof of this is sometimes difficult to obtain in the plants that are propagated vegetatively.

When self-compatible and self-incompatible plants are found and the latter prove to be highly seed-producing in certain crosses, as is the case with *Hemerocallis flava,* the evidence of incompatibilities is clear. The American strain of *Hemerocallis fulva* has sex organs that do function to some extent in certain inter-specific crosses and will, undoubtedly, produce abundant seed when it can be tested with stocks from a dif-

EXPLANATION OF PLATE

1. Pod of a plant of *H. flava;* the result of self-pollination showing that the plant is self-compatible.

2. Pod on same plant as 1; the result of controlled cross-pollination with pollen of *H. fulva.*

3. Seeds from such a pod as shown in 1 and 2; some ovules become mere rudiments of seeds and evidently are not fertilized; some embryos die during the development of seeds; some seeds develop fully and are viable.

4. Flowering branch of *H. fulva* near close of period of bloom. (*a*) Spur left when flowers fall. (*b*) Pod 10 days old, from cross with pollen of *H. Thunbergii,* but becoming wrinkled and about to fall. Occasionally such pods contain one or two partly developed seeds.

5. Mature pod of *H. fulva* from cross-pollination with *H. Thunbergii.* Such pods are rare. As far as known to the writer this is the first time the fruit of this species has been illustrated.

6, 7 and 8. All from a single plant of *H. Thunbergii.* All flowers carefully self-pollinated. Some pods (*a*) maturing and yielding a few viable seeds; some pods (*b*) becoming much shrivelled; no good pods on branch shown at 8. Results characteristic of feebly self-compatible plants of this species.

ferent seed source. But to obtain these, plants from widely different geographical sections or even wild plants from the native habitat may need to be secured.

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AN ORTHOTROPOUS OVULE IN *HYACINTHUS ORIENTALIS* L.

While sectioning ovaries of the hyacinth for embryo sacs one ovary was found which shows two irregularities. One of the ovules in the upper part of the ovary is orthotropous instead of anatropous. This ovule, as figure 1 shows, is typical in all other respects, the integuments, micropyle, nucellus, and embryo

Fig. 1

sac being well formed and apparently functional. In the median portion of the ovary the carpels seem to be incompletely fused and the placentas are slightly displaced (Fig. 2). Mas-